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How do changes in temperature during growth affect leaf pigment composition and photosynthesis in *Zea mays* genotypes differing in sensitivity to low temperature?

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Abstract

The changes in photosynthetic activity and composition of pigments induced by changes in temperature were examined in the third leaf of three chilling-tolerant and three chilling-sensitive genotypes of maize (*Zea mays* L.). The plants were grown under a controlled environment at a photon flux density of 550 µmol m^{-2} s^{-1}, a 12 h photoperiod and at a suboptimal temperature of 14/12 °C (day/night) until the full expansion of the third leaf. After this treatment, the chilling-tolerant genotypes, when compared with the sensitive ones, displayed a higher photosynthetic activity, a higher content of chlorophyll (Chl) *a*+*b*, a higher Chl *a/b* ratio, a larger total carotenoid pool size as well as a different carotenoid composition. When temperature was subsequently increased to 24/22 °C for 3 d the composition of the pigments changed, but the chilling-sensitive genotypes, while adjusting their lower Chl *a/b* ratio and their different carotenoid composition, were unable to adjust their lower content of chlorophyll, their smaller total carotenoid pool size or their lower photosynthetic performance. Moreover, while the chilling-tolerant genotypes converted the most part of zeaxanthin to violaxanthin in the xanthophyll cycle, the chilling-sensitive genotypes retained high amounts of zeaxanthin. The changes in pigment composition that occurred over the 3 d at 24/22 °C were largely conserved when the plants were returned to 14/12 °C, but photosynthetic activity decreased and zeaxanthin accumulated again. The results suggest that the capability of the chilling-tolerant genotypes, when compared with the sensitive ones, to retain high amounts of pigments and to form a competent photosynthetic apparatus at low temperature is the basis for their more vigorous growth in cool climates.

Key words: Carotenoids, chlorophylls, low temperature, photosynthesis, *Zea mays*.

Introduction

It is well established that when maize (*Zea mays* L.), a chilling-susceptible crop with a tropical/subtropical origin, is exposed to low temperature during growth the plants grow slowly and develop leaves with a reduced area and that have a pale green chlorotic appearance (Miedema, 1982; Stamp, 1984; Stamp *et al.*, 1983; Baker and Nie, 1994). The phenomenon of low temperature-induced chlorosis in maize is not yet fully understood, but it has been suggested that chlorosis develops under conditions of low temperature and high irradiance because chlorophyll is photo-oxidized prior to its integration in pigment–protein complexes of the thylakoid membranes where the pigments are less prone to photo-oxidative damage (MacWilliam and Naylor, 1967). It has been demonstrated that chilling-sensitive plant species, when compared with chilling-resistant ones, are highly susceptible to low temperature-induced photooxidations (Wise and Naylor, 1987; Wise, 1995). It is also well known that the carotenoids in general and those of the xanthophyll cycle in particular play an essential role in protecting the photosynthetic apparatus against photo-oxidative damage (Pfündel and Bilger, 1994; Demmig-Adams and Adams, 1996; Demmig-Adams *et al.*, 1996; Horton *et al.*, 1996; Yamamoto and Bassi, 1996; Gilmore, 1997).

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In temperate regions low temperature-induced chlorosis in maize is generally most pronounced in the early growing season. Leaves grown at low temperature, compared to those grown under normal conditions, are characterized by a very low photosynthetic performance (Nie and Baker, 1991; Stirling *et al*., 1991; Nie *et al*., 1992; Fryer *et al*., 1995; Haldimann *et al*., 1996), changes in the content and the composition of the pigments (Stamp *et al*., 1983; Nie and Baker, 1991; Nie *et al*., 1992; Haldimann *et al*., 1995, 1996; Haldimann, 1996, 1998), changes in the activities of several enzymes of photosynthetic carbon assimilation (Stamp, 1987) and oxygen scavenging system (Massacci *et al*., 1995; Hull *et al*., 1997; Fryer *et al*., 1998), reduced activities of photosystem I and photosystem II associated with modifications in the composition of thylakoid membranes (Nie and Baker, 1991; Bredenkamp and Baker, 1994; Robertson *et al*., 1993), and changes in the contents of the endogenous antioxidants ascorbate, glutathione and α-tocopherol (Leipner *et al*., 1997; Fryer *et al*., 1998). Leaf anatomy and the number and general structure of the chloroplasts have been shown not to be significantly different from those of leaves continually grown at normal growth temperature (Robertson *et al*., 1993). Perhaps even more important is the fact that low growth temperature-dependent depressions in the photosynthetic activity do not recover easily when the environmental conditions become favourable for growth. In fact, maize leaves thoroughly developed at low temperature exhibit a sustained low photosynthetic performance even after several days of growth in an optimal growth environment (Fryer *et al*., 1995; Nie *et al*., 1995; Haldimann, 1996). It is important to note that the effects of long-term moderate chilling are less dramatic and recovery from chilling-induced reductions in photosynthesis faster and more complete when the low temperature stress is imposed on maize leaves that were initially thoroughly developed under normal conditions (Haldimann, 1997). It appears therefore that the low growth temperature-dependent inhibition of the development of a competent photosynthetic apparatus is likely to be the most important factor responsible for the poor photosynthetic productivity of maize in cool climates (Baker, 1994; Baker *et al*., 1994).

It has been demonstrated that within the general susceptibility of maize to low temperature chilling-tolerant genotypes exist which, compared to more sensitive ones, have the capability to form a more competent photosynthetic apparatus when exposed to low temperature during growth (Stamp, 1984; Haldimann, 1998). Despite the numerous studies on the effects of chilling on the physiology of maize, the genotypic variability in the capacity to recover from low temperature-induced changes to the structure and the function of the photosynthetic apparatus has been largely neglected. This work, therefore, examines the changes in photosynthetic activity and composition of the pigments that occur in maize genotypes with different sensitivities to low temperature when, after an initial period of growth at low temperature, the plants experience a period with favourable growth conditions before being again exposed to low temperature.

Materials and methods

Plant material and growth conditions

Six *Zea mays* L. inbred lines were used in the experiments: chilling-tolerant Z7 (Breeding Company Zelder, Otterersum, The Netherlands), Z15 (Breeding Company Zelder, Otterersum, The Netherlands) and KW1074 (Kleinwanzlebener Saatzucht, Einbeck, Germany) with a European origin and chilling-sensitive MO17 (Experimental Station, University of Missouri, Columbia, Miss., USA), CM109 and Penjalinan (Suwan Farm, kasetsart University, Bangkok, Thailand) with a tropical/subtropical origin (Stamp *et al*., 1983; Stamp, 1984; Kocsy *et al*., 1996). Seeds were first germinated between moistened filter paper at 24 °C for 3 d. Seedlings were then planted into 1 dm^3 pots (2 plants per pot) containing a soil:peat mixture (5:1, v/v) and grown in a growth chamber (Conviron, model PGW36, Winnipeg, Canada) at a relative humidity of 60/70% (day/night), a 12 h photoperiod, and an irradiance of 550 µmol photons $m^{-2}\,s^{-1}$ (PAR). Light was provided by fluorescent tubes (Sylvania cool white, VHO) and incandescent bulbs (100 W, Sylvania). The plants were first grown at a suboptimal temperature of 14/12 °C (day/night) until the full development of the third leaf (45 d). Temperature was then increased from 14/12 °C to 24/22 °C for 3 d and subsequently returned to 14/12 °C for 5 d. Temperature changes took place during the night at a rate of about 0.85 °C h^{-1}. Photosynthetically active radiation (PAR) was measured with a quantum sensor (Li-185, Li-Cor, Lincoln, NE, USA). Canopy temperature in the growth chamber was measured with a psychrometer (type WVU) connected to a DL2 Delta Logger (Delta T Devices Ltd, Cambridge, UK).

Measurement of photosynthesis

The net rate of photosynthetic CO_2 assimilation (A_N) was measured 6 h after the beginning of the light period using the portable photosynthesis system Li-Cor 6200 (Li-Cor, Lincoln, NE, USA) under environmental conditions equivalent to those which predominate during growth.

Pigment analysis

For pigment analysis two leaf segments (1.5 cm^2) were cut from the central part of the third leaf, frozen immediately in liquid nitrogen, and subsequently stored in a freezer at −80 °C until analysis. Plant material was collected 6 h after the beginning of the light period. Pigment extraction and high performance liquid chromatography (HPLC) analyses of chlorophylls and carotenoids were carried out essentially according to Thayer and Björkman (1990) as described elsewhere (Haldimann *et al*., 1995).

Statistics

All the measurements were made on six replicates. The significance ($P<0.05$) of the differences in photosynthetic activity and contents of pigments observed among the genotypes was tested with analysis of variance using the STATGRAPHICS statistical system (STSC Inc., MA, USA).

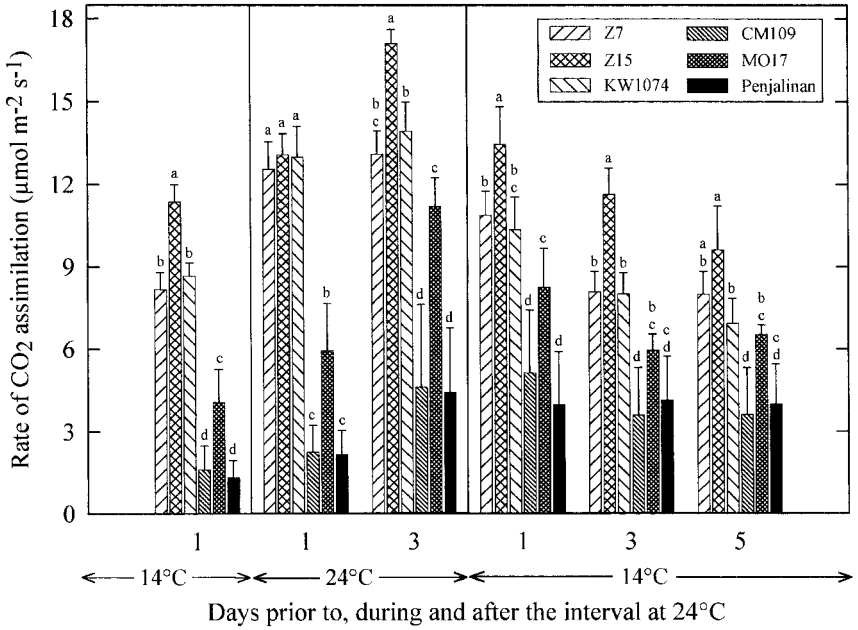

Fig. 1. Effects of changes in temperature on the net rate of photosynthetic CO_2 assimilation in the third leaf of three chilling-tolerant (Z7, Z15 and KW1074) and three chilling-sensitive (CM109, MO17 and Penjalinan) genotypes of *Zea mays*. The plants were initially grown at a suboptimal temperature of 14/12 °C until the full expansion of the third leaf. Values are means of six replicates. Bars indicate SD. Within a given day of measurement values carrying different letters are significantly different at $P<0.05$.

Results

Photosynthetic activity

The chilling-tolerant genotypes (Z7, Z15 and KW1074) showed a much higher net rate of CO_2 assimilation (A_N) than the chilling-sensitive ones (CM109, MO17 and Penjalinan) when the third leaf of the plants had achieved full expansion after having been continually exposed to 14/12 °C (day/night) during growth (Fig. 1). The A_N increased in all the genotypes when the temperature was increased to 24/22 °C, but the chilling-sensitive genotypes were not able to take full advantage of the warmer conditions to increase their inferior photosynthetic activity although the A_N in MO17 approached that of the chilling-tolerant genotypes on the third day at 24/22 °C. When the plants were returned to 14/12 °C a reduction in the A_N could be observed in most of the genotypes during the first 3 d after the temperature change, but thereafter photosynthetic activity stabilized at a low level (Fig. 1). During this second period at 14/12 °C the chilling-tolerant genotypes still exhibited a higher A_N than the chilling-sensitive ones, but the differences between MO17 and Z7 or KW1074 were not any more stastistically significant (Fig. 1).

Content of chlorophyll and total carotenoid pool size

At the third leaf stage, before the temperature was increased to 24/22 °C, the chilling-tolerant genotypes exhibited a higher content of chlorophyll (Fig. 2A) and a higher Chl *a*/*b* ratio (Fig. 2B) than the chilling-sensitive ones. Likewise, the total carotenoid pool size was generally larger in the chilling-tolerant genotypes than in the sensitive ones when expressed on a unit leaf area basis (Fig. 3A). No clear difference appeared between the two categories of genotypes when the total carotenoid content was expressed relative to the content of chlorophyll (Fig. 3B). The content of chlorophyll increased when the temperature was increased to 24/22 °C, but the chlorophyll content of the chilling-sensitive genotypes stayed significantly below that of the chilling-tolerant ones (Fig. 2A). At warmer conditions there was also an increase in the Chl *a*/*b* ratio and on the third day at 24/22 °C this ratio was similar in most of the genotypes (Fig. 2B). Since the content of total carotenoid (Fig. 3A) was affected by the temperature change to a much lesser extent than the content of chlorophyll (Fig. 2A), the ratio of total carotenoid to Chl $a+b$ decreased markedly during the treatment at 24/22 °C (except in Z15 and KW1074 where the changes were less pronounced) and on the third day at 24/22 °C this ratio became similar in all the genotypes (Fig. 3B). During the second period at 14/12 °C the chilling-tolerant genotypes still showed a higher content of chlorophyll (Fig. 2A) and a larger total carotenoid pool size (Fig. 3A) than the chilling-sensitive ones, but the two categories of genotypes showed no clear difference in terms of their Chl *a*/*b* ratio (Fig. 2B) or their ratio of total carotenoid to Chl $a+b$ (Fig. 3B).

Components of the carotenoid pool

When the plants had been continually exposed to low temperature during growth a genotypic variability

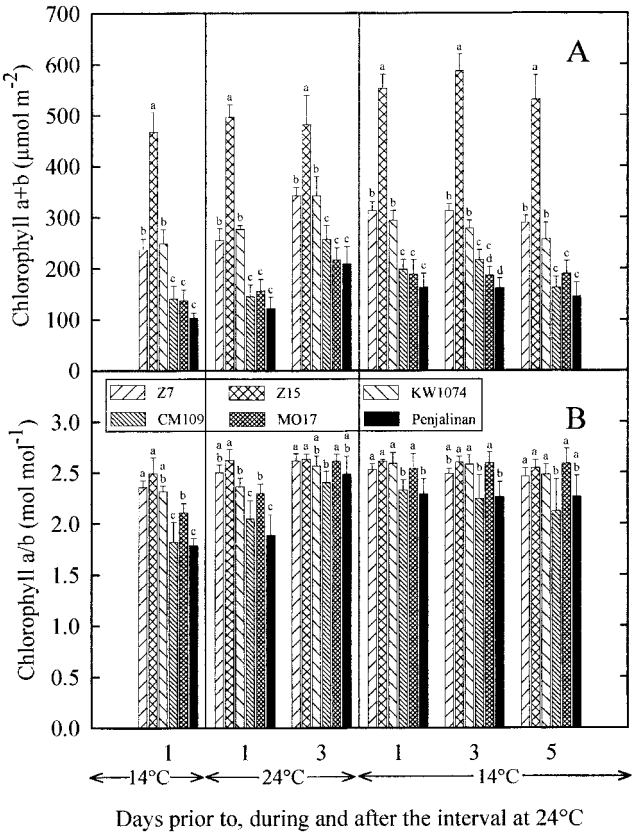

Fig. 2. Effects of changes in temperature on the content of chlorophyll (Chl) (A) and the Chl *a*/*b* ratio (B) in the third leaf of three chilling-tolerant (Z7, Z15 and KW1074) and three chilling-sensitive (CM109, MO17 and Penjalinan) genotypes of *Zea mays*. The plants were initially grown at a suboptimal temperature of 14 °C until the full expansion of the third leaf. Values are means of six replicates. Bars indicate SD. Within a given day of measurement values carrying different letters are significantly different at $P<0.05$.

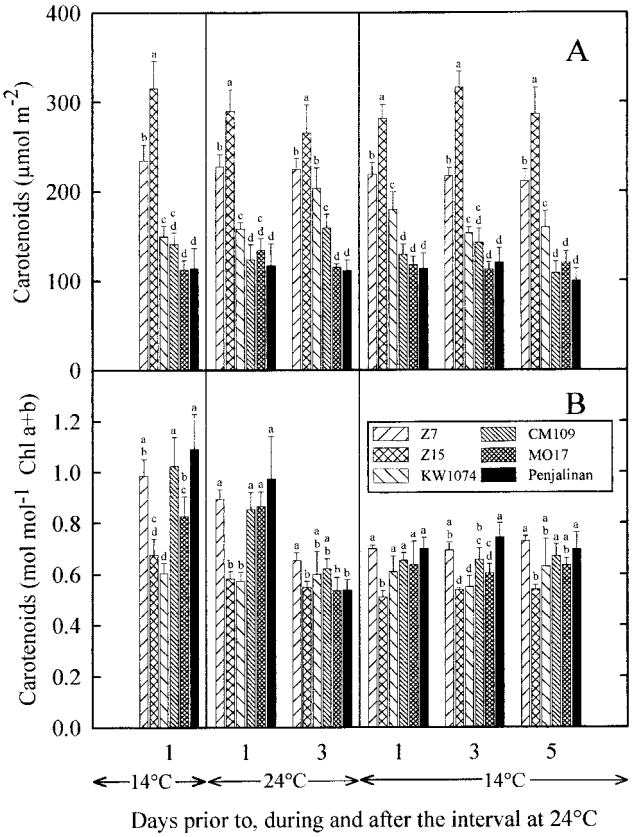

Fig. 3. Effects of changes in temperature on the total carotenoid pool size expressed either on a unit leaf area basis (A) or relative to the total chlorophyll content (B) in the third leaf of three chilling-tolerant (Z7, Z15 and KW1074) and three chilling-sensitive (CM109, MO17 and Penjalinan) genotypes of *Zea mays*. See Fig. 2 for more details.

appeared in the contents of lutein, neoxanthin, β-carotene, and xanthophyll cycle carotenoids (violaxanthin (V)+antheraxanthin (A)+zeaxanthin (Z)) regardless of whether the content of pigment was expressed relative to the content of chlorophyll (Fig. 4A–D) or the total carotenoid pool size (Fig. 5A–D). However, concerning the ratio of neoxanthin to Chl $a+b$ none of the differences that appeared among the genotypes was statistically significant (Fig. 4B). The chilling-tolerant genotypes, when compared with the sensitive ones, displayed a higher relative content of β-carotene (Fig. 5C) and a lower ratio of V+A+Z to β-carotene (Fig. 6), but the differences between Z7 and MO17 were not statistically significant. Increasing the temperature changed the carotenoid composition. In particular, there was a decrease in the ratios of lutein and V+A+Z to Chl $a+b$ (Fig. 4A, D), a decrease in the relative content of V+A+Z (Fig. 5D), an increase in the relative content of β-carotene (Fig. 5C), and a decrease in the ratio of V+A+Z to β-carotene (Fig. 6). All these changes were less pronounced in Z15 and KW1074 than in the other genotypes. On the third day at 24/22 °C, the two categories of genotypes no longer showed a clear difference in terms of their relative content of β-carotene (Fig. 5C) or their ratio of V+A+Z to β-carotene (Fig. 6), but the chilling-tolerant genotypes displayed a higher ratio of β-carotene to Chl $a+b$ than the chilling-sensitive ones (Fig. 4C). More generally, at warmer conditions, the amplitude of the genotypic variability in the contents of the different components of the carotenoid pool was reduced regardless of whether the content of pigment was expressed relative to the chlorophyll content (Fig. 4A–D) or the total carotenoid pool size (Fig. 5A–D). The changes in the contents of the different components of the carotenoid pool that occurred over the 3 d at warmer conditions were largely conserved over the following 5 d at 14/12 °C (Figs 4, 5). Thus, the amplitude of the genotypic variability remained reduced and the two categories of genotypes showed no clear difference in terms of their carotenoid composition (Figs 4, 5, 6).

Xanthophyll cycle carotenoids

The analysis of the effects of changes in temperature on the composition of the xanthophyll cycle pool (V+A+Z) revealed that prior to the increase of the temperature to

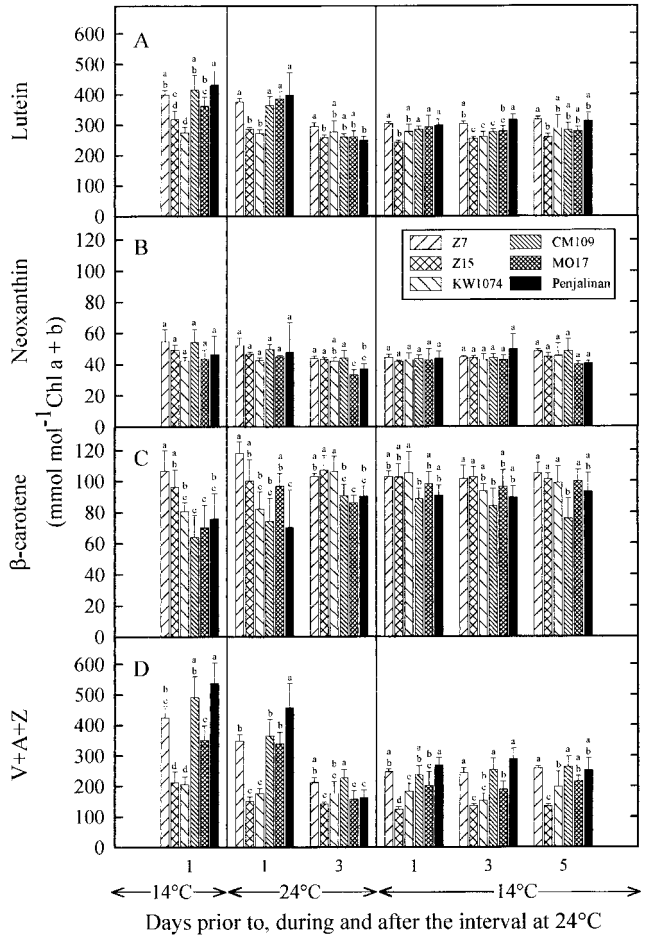

Fig. 4. Effects of changes in temperature on contents of lutein (A), neoxanthin (B), β-carotene (C) and xanthophyll cycle carotenoids (V+A+Z) (D) expressed relative to the total chlorophyll content in the third leaf of three chilling-tolerant (Z7, Z15 and KW1074) and three chilling-sensitive (CM109, MO17 and Penjalinan) genotypes of *Zea mays*. V, A, and Z denote the contents of violaxanthin, antheraxanthin and zeaxanthin, respectively. See Fig. 2 for more details.

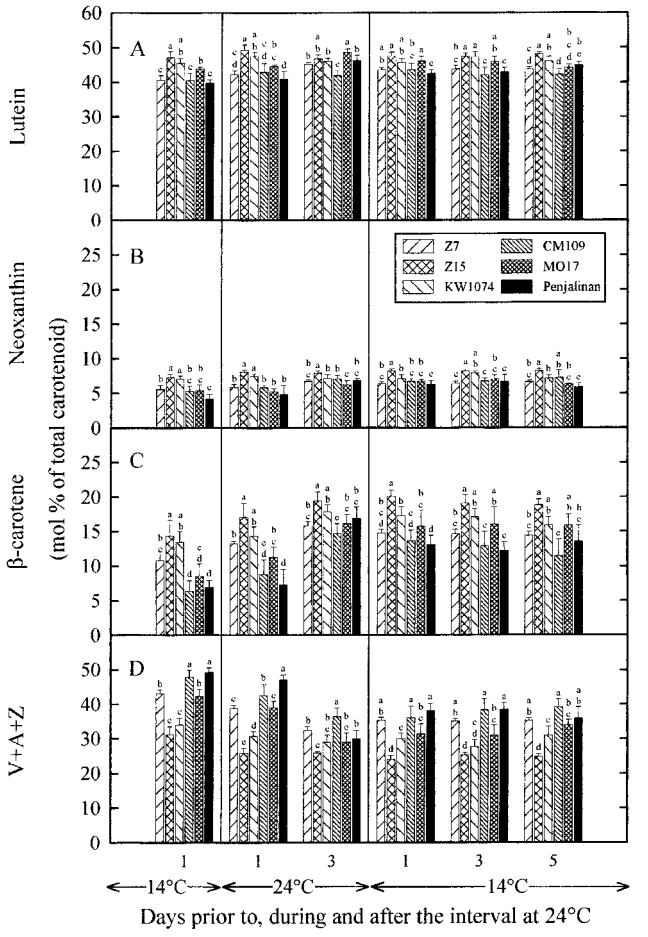

Fig. 5. Effects of changes in temperature on contents of lutein (A), neoxanthin (B), β-carotene (C) and xanthophyll cycle carotenoids (V+A+Z) (D) expressed as a percentage of the total carotenoid pool size in the third leaf of three chilling-tolerant (Z7, Z15 and KW1074) and three chilling-sensitive (CM109, MO17 and Penjalinan) genotypes of *Zea mays*. V, A, and Z denote the contents of violaxanthin, antheraxanthin and zeaxanthin, respectively. See Fig. 2 for more details.

24/22 °C zeaxanthin accounted for about 80–90% and 40–60% of the pool in the chilling-sensitive genotypes and the chilling-tolerant ones, respectively (Fig. 7C). The relative content of antheraxanthin was significantly higher in the chilling-tolerant genotypes (18–21%) than in the chilling-sensitive ones (6–10%) (Fig. 7B). On the first day at 24/22 °C, zeaxanthin was largely converted to violaxanthin in the chilling-tolerant genotypes, whereas in the chilling-sensitive ones much less conversion took place with the result that zeaxanthin accounted for about 15–20% of the V+A+Z pool in the former genotypes while this portion was still around 60% (CM109 and MO17) or 80% (Penjalinan) in the latter genotypes (Fig. 7A-C). Even on the third day at 24/22 °C, zeaxanthin still accounted for 30% (MO17) or 40% (CM109 and Penjalinan) of the V+A+Z pool in the chilling-sensitive genotypes while the portion of zeaxanthin had fallen below 12% in the chilling-tolerant ones (Fig. 7C). When the plants were subsequently returned to 14/12 °C violaxanthin was de-epoxidized to zeaxanthin, but the relative content of zeaxanthin was always significantly higher in the chilling-sensitive genotypes than in the tolerant ones (Fig. 7A, C).

Discussion

Photosynthetic activity increased in all the maize genotypes when the temperature was increased from 14/12 °C to 24/22 °C (Fig. 1). However, even on the third day at warmer conditions, the rate of CO_2 assimilation stayed much below that measured in the same genotypes when the plants were continually developed at 24/22 °C (about 25 μmol CO_2 m^{-2} s^{-1}; see Haldimann, 1998). Moreover, the treatment at 24/22 °C did not permit the chilling-sensitive genotypes to adjust their inferior photosynthetic performance (Fig. 1). It has been demonstrated that

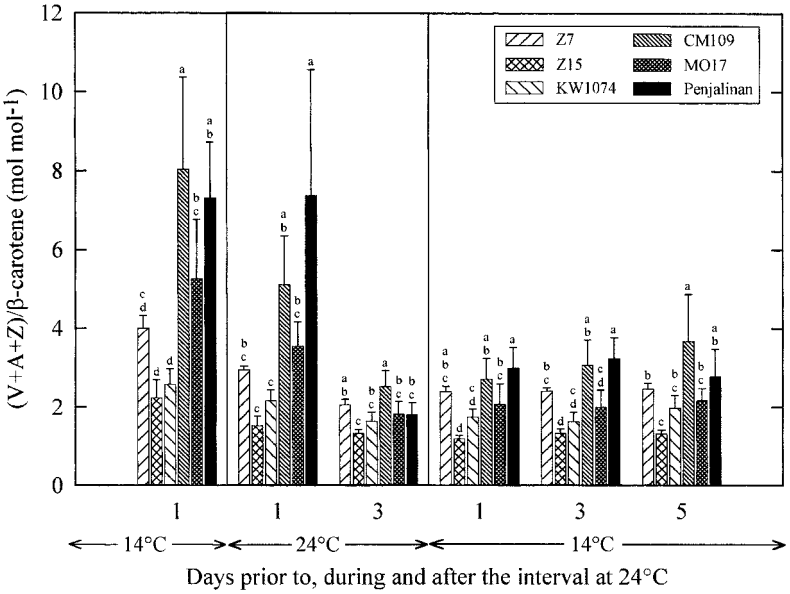

Fig. 6. Effects of changes in temperature on the ratio of total xanthophyll cycle carotenoids (V+A+Z) to β-carotene in the third leaf of three chilling-tolerant (Z7, Z15 and KW1074) and three chilling-sensitive (CM109, MO17 and Penjalinan) genotypes of *Zea mays*. V, A, and Z denote the contents of violaxanthin, antheraxanthin and zeaxanthin, respectively. See Fig. 2 for more details.

young leaf tissue, in which the photosynthetic apparatus is still under development, is better able to recover from low growth temperature-induced depressions in photosynthetic activity than mature leaf tissue (Haldimann, 1996). Thus, it is possible that the comparatively large increase in photosynthetic activity observed in MO17 at warmer conditions is related to the fact that the third leaf of this genotype was not yet fully mature when the temperature was increased as this genotype was growing very slowly at low temperature. The chilling-sensitive genotypes, starting from a lower content of chlorophyll (Fig. 2A) and a smaller total carotenoid pool size (Fig. 3A) than the chilling-tolerant genotypes, were not able to compensate for these deficiencies during the treatment at 24/22 °C. This is likely to be an important factor responsible for the permanent weak photosynthetic performance observed in the chilling-sensitive genotypes (Fig. 1).

As discussed in more detail elsewhere (Haldimann, 1998), the reduced Chl *a*/*b* ratio (Fig. 2B) together with the reduced content of β-carotene (Figs 4C, 5C) observed in maize leaves grown at low temperature is likely to be related to the fact that such leaves display reduced proportions of reaction centre core complexes to light-harvesting antenna complexes in photosystem I (PSI) and photosystem II (PSII) (Nie and Baker, 1991). This feature is associated with reduced electron transport activities in both photosystems (Nie and Baker, 1991; Nie *et al.*, 1995). As the activities of both photosystems have been shown to increase when the plants are exposed to warmer conditions (Nie *et al.*, 1995), the increase in the Chl *a*/*b* ratio (Fig. 2B) and the increase in the content of β-carotene (Figs 4C, 5C) together with the less marked changes in the contents of lutein (Fig. 5A) and neoxanthin (Fig. 5B) that occurred on exposure of the plants to warmer conditions have been thought indicative for a preferential resynthesis of PSI and PSII reaction centre core complexes relative to light-harvesting antenna complexes (Haldimann, 1996). Maize has two types of chloroplasts, mesophyll and bundle sheath, with different PSII/PSI compositions. Thus, since it has been demonstrated that large amounts of β-carotene are associated with PSI and that PSI displays a high Chl *a*/*b* ratio (Thayer and Björkman, 1992), it is also possible that changes in the composition of the pigments reflect differential changes in these two populations of chloroplasts.

The finding that at low temperature the chilling-sensitive genotypes generally displayed a lower Chl *a*/*b* ratio (Fig. 2B) and a lower content of β-carotene (Figs 4C, 5C) than the chilling-tolerant genotypes might be indicative of a higher proportion of damaged reaction centres in the former genotypes than in the latter ones. However, since the chilling-sensitive genotypes had the capability to adjust their lower Chl *a*/*b* ratio (Fig. 2B) and their lower content of β-carotene (Figs 4C, 5C) at warmer conditions, it appears that efficient mechanisms of repair were operating in these genotypes, but that they did not permit these genotypes to adjust their inferior photosynthetic competence (Fig. 1). That the chilling-sensitive genotypes displayed a higher ratio of V+A+Z to β-carotene than the chilling-tolerant ones when the plants had been continually exposed to low temperature during growth (Fig. 6) may reflect some differences in the structure of PSII and PSI. Indeed, β-carotene is mainly localized in the reaction centre core complexes of PSII

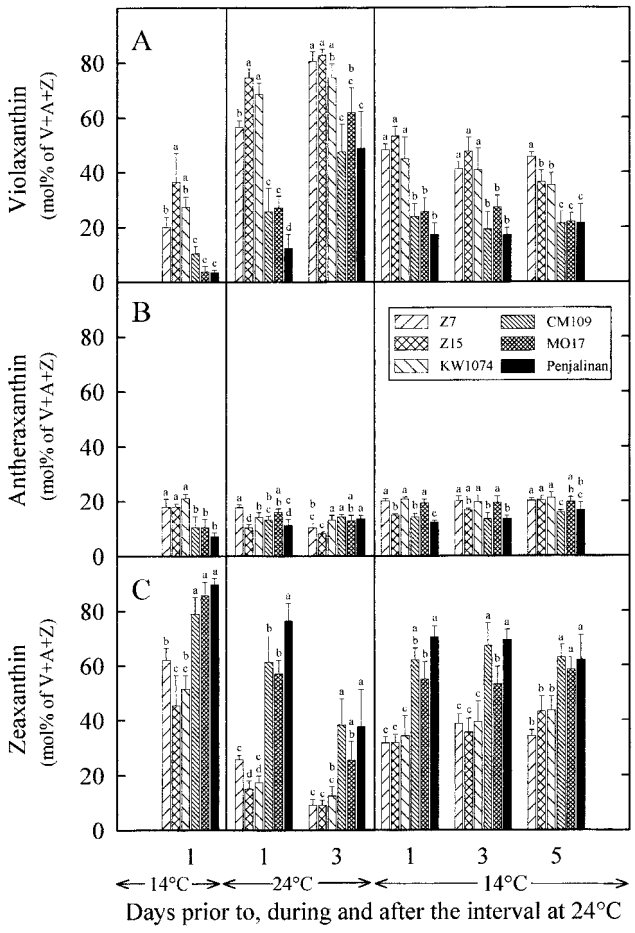

Fig. 7. Effects of changes in temperature on the relative contents of violaxanthin (A), antheraxanthin (B) and zeaxanthin (C) within the xanthophyll cycle pool (V+A+Z) in the third leaf of three chilling-tolerant (Z7, Z15 and KW1074) and three chilling-sensitive (CM109, MO17 and Penjalinan) genotypes of *Zea mays*. See Fig. 2 for more details.

and PSI, whereas the xanthophyll cycle components are predominantly associated with light-harvesting antenna complexes and thought to be enriched in some minor pigment–protein complexes within PSII antenna (Yamamoto and Bassi, 1996). However, the two categories of genotypes no longer showed a difference in terms of their ratio of V+A+Z to β-carotene on the third day at warmer conditions (Fig. 6). More generally, the exposure of maize plants grown at low temperature to warmer conditions greatly reduced or almost eliminated the low temperature-induced genotypic variability in the composition of the pigments (Figs 2B, 3B, 4A–D, 5A–D). Reduced genotypic variability in the composition of the pigments was largely preserved when the plants were returned to 14/12 °C as the changes in pigment composition that occured over the 3 d at 24/22 °C were largely conserved over the following 5 d at 14/12 °C (Figs 2B, 3B, 4A–D, 5A–D). The reason why, despite the accumulation of chlorophyll (Fig. 2A), the increase in the Chl *a*/*b* ratio (Fig. 2B), the adjustment of the carotenoid composition (Figs 4, 5, 6) and, more generally, of the composition of the thylakoid membranes (Nie *et al.*, 1995) maize leaves grown at low temperature are incapable of achieving full photosynthetic competence when exposed to warmer conditions remains an open question, but the organization and stability of proteins in the membranes may play a central role (Nie *et al.*, 1995).

The plants responded to the low temperature stress by reducing their chlorophyll content (Fig. 2A), increasing their ratio of total carotenoid to chlorophyll (Fig. 3B) and by the accumulation of large amounts of zeaxanthin and antheraxanthin (Fig. 7B, C). This leads to a reduction in the absorption of excitation energy on one hand and to an increase in the capacity for non-radiative energy dissipation on the other hand. Differences in the ratio of total carotenoid to chlorophyll (Fig. 3B) and in the accumulation of zeaxanthin (Fig. 7C) that appeared among the genotypes prior to the treatment at 24/22 °C, the content of zeaxanthin being higher in the chilling-sensitive genotypes than in the tolerant ones, may reflect differences in the need to dissipate excitation energy that cannot be dissipated through the electron transport chain. As expected, the ratio of total carotenoid to chlorophyll (Fig. 3B) and the content of zeaxanthin (Fig. 7C) decreased as photosynthetic activity increased (Fig. 1) at warmer conditions. However, even at warmer conditions the chilling-sensitive genotypes retained higher amounts of zeaxanthin than the chilling-tolerant ones (Fig. 7C). Zeaxanthin accumulated again when the plants were returned to 14/12 °C, but here again the content of zeaxanthin was higher in the chilling-sensitive genotypes than in the tolerant ones (Fig. 7C). Collectively these results suggest that the requirement of excitation energy dissipation was generally higher in the chilling-sensitive genotypes than in the tolerant ones.

In conclusion, none of the maize genotypes tested in this study had the capacity to recover fully from low temperature-induced depressions in photosynthetic activity when the plants were exposed to warmer conditions. Nevertheless, the chilling-tolerant genotypes, when compared with the chilling-sensitive ones, had the capability to accumulate higher amounts of pigments and to form a more competent photosynthetic apparatus at low temperature. Warmer conditions permitted the chilling-sensitive genotypes to adjust their carotenoid composition, but neither their lower content of pigment nor their inferior photosynthetic performance. Thus, the capacity of the chilling-tolerant genotypes to form a more competent photosynthetic apparatus at low temperature is likely to be an important factor responsible for their more vigorous growth in cool climates.

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References

Baker NR. 1994. Chilling stress and photosynthesis. In: Alscher RG, Hess JL, eds. *Antioxidants in higher plants*. Boca Raton, Florida: CRC Press, 127–154.

Baker NR, Nie GY. 1994. Chilling sensitivity of photosynthesis in maize. In: Bajaj YPS, ed. *Biotechnology in agriculture and forestry*: *maize*, Vol. 9. Berlin: Springer-Verlag, 465–481.

Baker NR, Farage PK, Stirling CM, Long SP. 1994. Photoinhibition of crop photosynthesis in the field at low temperatures. In: Baker NR, Bowyer JR, eds. *Photoinhibition of photosynthesis, from molecular mechanisms to the field*. Oxford: BIOS Scientific Publishers, 349–363.

Bredenkamp GJ, Baker NR. 1994. Temperature-sensitivity of D1 protein metabolism in isolated *Zea mays* chloroplasts. *Plant, Cell and Environment* **17,** 205–210.

Demmig-Adams B, Adams III WW. 1996. The role of xanthophyll cycle carotenoids in the protection of photosynthesis. *Trends in Plant Science* **1,** 21–26.

Demmig-Adams B, Gilmore AM, Adams III WW. 1996. *In vivo* functions of carotenoids in higher plants. *The FASEB Journal* **10,** 403–412.

Fryer MC, Oxborough K, Martin B, Ort DR, Baker NR. 1995. Factors associated with depression of photosynthetic quantum efficiency in maize at low growth temperature. *Plant Physiology* **108,** 761–767.

Fryer MJ, Andrews JR, Oxborough K, Blowers DA, Baker NR. 1998. Relationship between CO_2 assimilation, photosynthetic electron transport, and active O_2 metabolism in leaves of maize in the field during periods of low temperature. *Plant Physiology* **116,** 571–580.

Gilmore AM. 1997. Mechanistic aspects of xanthophyll cycle-dependent photoprotection in higher plant chloroplasts and leaves. *Physiologia Plantarum* **99,** 197–209.

Haldimann P. 1996. Effects of changes in growth temperature on photosynthesis and carotenoid composition in *Zea mays* leaves. *Physiologia Plantarum* **97,** 554–562.

Haldimann P. 1997. Chilling-induced changes to carotenoid composition, photosynthesis and the maximum quantum yield of photosystem II photochemistry in two maize genotypes differing in tolerance to low temperature. *Journal of Plant Physiology* **151,** 610–619.

Haldimann P. 1998. Low growth temperature-induced changes to pigment composition and photosynthesis in *Zea mays* genotypes differing in chilling sensitivity. *Plant, Cell and Environment* **21,** 200–208.

Haldimann P, Fracheboud Y, Stamp P. 1995. Carotenoid composition in *Zea mays* developed at sub-optimal temperature and different light intensities. *Physiologia Plantarum* **95,** 409–414.

Haldimann P, Fracheboud Y, Stamp P. 1996. Photosynthetic performance and resistance to photoinhibition of *Zea mays* L. leaves grown at sub-optimal temperature. *Plant, Cell and Environment* **19,** 85–92.

Horton P, Ruban AV, Walters RG. 1996. Regulation of light harvesting in green plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **47,** 655–684.

Hull MR, Long SP, Jahnke LS. 1997. Instantaneous and developmental effects of low temperature on the catalytic properties of antioxidants enzymes in two *Zea* species. *Australian Journal of Plant Physiology* **24,** 337–343.

Kocsy G, Brunner M, Ruegsegger A, Stamp P, Brunold C. 1996. Glutathione synthesis in maize genotypes with different sensitivities to chilling. *Planta* **198,** 365–370.

Leipner J, Fracheboud Y, Stamp P. 1997. Acclimation by suboptimal growth temperature dimishes photooxidative damage in maize leaves. *Plant, Cell and Environment* **20,** 366–372.

MacWilliam JR, Naylor AW. 1967. Temperature and plant adaptation. I. Interaction of temperature and light in synthesis of chlorophyll in corn. *Plant Physiology* **95,** 184–195.

Massacci A, Iannelli MA, Pietrini F, Loreto F. 1995. The effect of growth at low temperature on photosynthetic characteristics and mechanisms of photoprotection of maize leaves. *Journal of Experimental Botany* **46,** 119–127.

Miedema P. 1982. The effects of low temperature on *Zea mays*. *Advances in Agronomy* **35,** 93–128.

Nie GY, Baker NR. 1991. Modification to thylakoid composition during development of maize leaves at low growth temperature. *Plant Physiology* **95,** 184–191.

Nie GY, Long SP, Baker NR. 1992. The effects of development at sub-optimal growth temperature on photosynthetic capacity and susceptibility to chilling-dependent photoinhibition in *Zea mays*. *Physiologia Plantarum* **85,** 554–560.

Nie GY, Robertson EJ, Fryer MJ, Leech RM, Baker NR. 1995. Response of the photosynthetic apparatus in maize leaves grown at low temperature to transfer to normal growth temperature. *Plant, Cell and Environment* **18,** 1–12.

Pfündel EE, Bilger W. 1994. Regulation and possible function of the violaxanthin cycle. *Photosynthesis Research* **42,** 89–109.

Robertson EJ, Baker NR, Leech RM. 1993. Chloroplast thylakoid protein changes induced by low growth temperature in maize revealed by immunocytology. *Plant, Cell and Environment* **16,** 809–818.

Stamp P. 1984. Chilling tolerance of young plants demonstrated on the example of maize (*Zea mays* L.). *Journal of Agronomy and Crop Science* **7,** (supplement) 1–83.

Stamp P. 1987. Photosynthetic traits of maize genotypes at constant and fluctuating temperature. *Plant Physiology and Biochemistry* **25,** 729–733.

Stamp P, Thiraporn, R, Geisler G. 1983. Adaptation to sub- and supraoptimal temperature of inbred maize lines differing in origin with regard to seedling development and photosynthetic traits. *Physiologia Plantarum* **58,** 62–68.

Stirling CM, Nie GY, Aguilera C, Nugawela A, Long SP, Baker NR. 1991. Photosynthetic productivity of an immature maize crop: changes in quantum yield of CO_2 assimilation, conversion efficiency and thylakoid proteins. *Plant, Cell and Environment* **14,** 947–954.

Thayer SS, Björkman O. 1990. Leaf xanthophyll content and composition in sun and shade determined by HPLC. *Photosynthesis Research* **23,** 331–343.

Thayer SS, Björkman O. 1992. Carotenoid distribution and de-epoxidation in thylakoid pigment–protein complexes from cotton and bundle-sheath cells of maize. *Photosynthesis Research* **33,** 213–225.

Wise RR. 1995. Chilling-enhanced photo-oxidation: the production, action and study of reactive oxygen species produced during chilling in the light. *Photosynthesis Research* **45,** 79–97.

Wise RR, Naylor AW. 1987. Chilling-enhanced photo-oxidation. Evidence for the role of singlet oxygen and superoxide in the breakdown of pigments and endogenous antioxidants. *Plant Physiology* **83,** 278–282.

Yamamoto HY, Bassi R. 1996. Carotenoids: localization and function. In: Ort DR, Yocum CF, eds. *Oxygenic photosynthesis: the light reactions*. Advances in Photosynthesis, Vol. 4. Dordrecht: Kluwer Academic Publishers, 539–563.